

A NEW *ZAMIA* (ZAMIACEAE, CYCADALES) FROM CENTRAL PANAMA

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ABSTRACT

Zamia elegantissima Schutzman, Vovides, & Adams is described from central Panamá, and differentiated from closely related taxa *Z. fairchildiana* L.D. Gómez and *Z. tuerckheimii* J. Donn. Sm. The new species was previously considered part of *Z. fairchildiana*, but is morphologically and geographically distinct.

KEY WORDS: *Zamia*, Zamiaceae, cycad, taxonomy, systematics

INTRODUCTION

Whereas a proliferation of names caused confusion in earlier cycad taxonomies, especially *Zamia*, confusion regarding the identity of Panamanian and Costa Rican cycads have resulted mostly from scant and misinterpreted communications between workers. The well-known systematist Robert L. Dressler noticed the variation in the native Panamanian species of *Zamia* during his long-standing studies of orchids, and communicated some of his thoughts to other workers over the years. Unfortunately, none of them did the necessary fieldwork and other systematic study to develop a thorough, comprehensive treatment. The result of this was primarily the existence of unrecognized or improperly delimited species, one of which we highlight here.

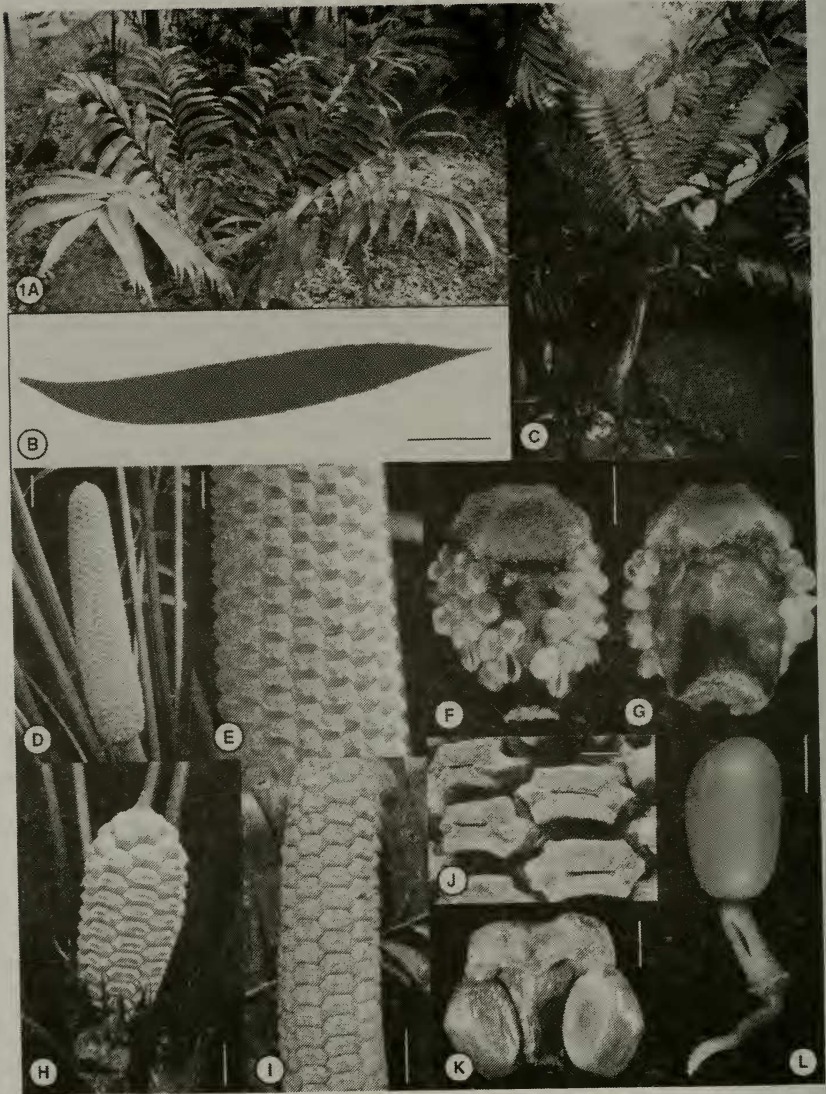


Figure 1. *Zamia elegantissima* Schutzman, Vovides, & Adams, *spec. nov.* A. habit of cultivated plant. B. leaflet. C. plant in habitat. D. microstrobilus. E. microstrobilus detail. F. abaxial surface of microsporophyll. G. adaxial surface of microsporophyll. H. emerging megastrobilus. I. large megastrobilus in habitat. J. megasporophyll. K. mature megasporophyll with seeds. L. germinating seed (scales for B,D,H = 3 cm; E,J,K,L = 1 cm; F,G = 3 mm; H = 5 cm).

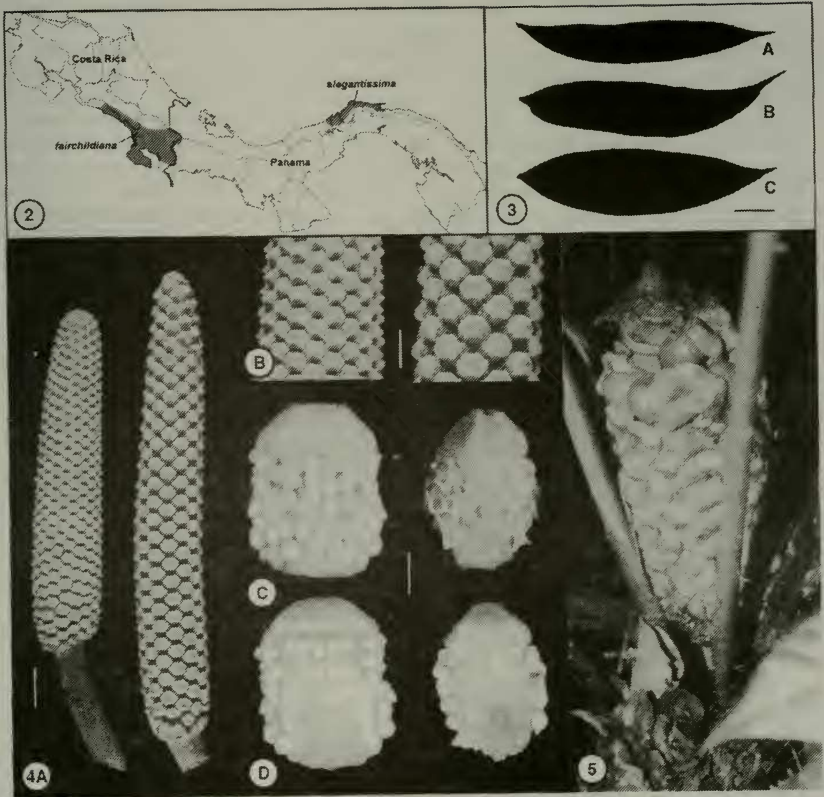


Figure 2. Distribution of *Zamia fairchildiana* and *Z. elegantissima* in Panamá and Costa Rica.

Figure 3. Comparison of average leaflets: A) *Zamia elegantissima*, B) *Z. fairchildiana*, C) *Z. tuerckheimii* (scale = 3 cm).

Figure 4. Comparisons between *Zamia fairchildiana* (left side) and *Z. elegantissima* (right side). A. microstrobilus (scale = 2 cm); B. microstrobilus detail (scale = 1 cm); C. abaxial microsporophyll surface (scale = 3 mm); D. adaxial microsporophyll surface (scale = 3 mm).

Figure 5. *Zamia fairchildiana* mature megastrobilus showing megasporophylls not folded back toward strobilar axis.

Dressler had by the late 1970's rediscovered the then "nearly mythical epiphyte" *Zamia pseudoparasitica* Warscz. in Veraguas, Panamá. He also informally referred to a *Z. "pseudo-pseudoparasitica"*, a little-known plant that was actually quite common in Central Panamá, but confused with *Z. pseudoparasitica*. This central Panamanian plant was not an epiphyte, but an arborescent plant, with trunks often reaching three meters in height. Knowing that this terrestrial species of *Zamia* was undescribed, Dressler's intention was to name it for "Sandy" (Dr. A.G.B.) Fairchild. Dr. Fairchild was a well-known Isthmian entomologist and naturalist, in whose garden Dressler had observed several of the Panamanian cycads. He also was the son of David Fairchild, the famous, well-published plant explorer in the earlier part of the twentieth century and namesake of Fairchild Tropical Garden in Coral Gables, Florida. In an unpublished synopsis of Panamanian taxa, Dressler mentioned that he had wanted to avoid putting the name in writing before he actually described the species. Robert Wilson of the Las Cruces Botanical Garden in eastern Costa Rica, however, must have heard the name and assumed that the plants from his area belonged to the same species, because he distributed seeds and labeled them "*Z. fairchildii*." Gómez published the epithet in *Phytologia* in 1982, typifying the species with a specimen from a population of plants in the Osa Peninsula in southeastern Costa Rica. He included no etymology, but did mention to other workers, notably Dr. Knut Norstog (Norstog, pers. comm.) that he had named it after David Fairchild. The Costa Rican plants, which occur from sea level to 1500 m in elevation in southeastern to central Costa Rica and also in extreme Western Panamá, are only superficially similar to the central Panamanian plants, and are themselves a unique species.

Seed were collected in 1983 and 1984 from along the Río Iguanita in Colón Province, and these have since grown to reproductive size. Microstrobili were produced in 1996 and megastrobili in 1997. The differences between Gómez' *Zamia fairchildiana* and this Panamanian endemic became obvious from the eophyll (first seedling leaf) stage.

Stevenson, in his treatment of Panamanian zamias (1993), did not recognize the Panamanian populations as distinct. In it, the range of *Zamia fairchildiana* is given as sporadic from southeastern Costa Rica to Cuna Yala in eastern Panamá. Further investigation has not turned up populations of either the Costa Rican or Panamanian entity in the large intervening area between known populations (Figure 2). So far as we know, the Panamanian species is exclusively found on the Atlantic and *Z. fairchildiana* on the Pacific side of the Sierra de Talamanca. So, the epithet *fairchildiana*, with which Dressler wished to honor Dr. A.G.B. Fairchild, graces a different species and informally honors David Fairchild instead. The plant from central Panamá, which Dressler intended to describe, is therefore nameless, a condition we remedy here.

Zamia elegantissima Schutzman, Vovides, & Adams, *spec. nov.* (Figures 1a-l). -
TYPE: PANAMA. Colón, Dressler 4897 (MO,PMA).

Haec species *Zamia fairchildianae* L.D. Gómez affinis sed folioliis plerumque apice usque ad medium dentatis, folioliis non leviter carinatis, margine megasporophyllorum retroflexis, apice microsporophyllorum quasi

pyramidalis, tantum microsporangiis in superficiebus abaxialis microsporophyllii, et seminibus maturis non visibilis inter megasporophylla.

Description. Plants large, arborescent with trunks to 3 m. Leaves usually many (30 or more in cultivation), upright, to 170 cm long; leaflets lanceolate and slightly falcate, 20-22 cm long, 2.5-4.0 cm wide; apex short but not abruptly acuminate; margin denticulate from approximately the midpoint of the margin; marginal teeth 0.5-1.5 mm long; base attenuate, apple green when expanding, bright green, glabrous, and shining when mature; articulation with rachis 3-6 mm wide; petioles nearly unarmed, 43-44 cm long; prickles small and terete when present. Microsporangiate strobili erect, cylindrical, beige-yellow to light brown with green undertones; peduncle puberulent; microsporophylls oblong-obtriangular, the distal ends with protruding hexagonal faces; microsporangia covering abaxial surface of microsporophylls and absent on adaxial surface. Megasporangiate cylindrical with large pointed or rounded apiculate apex, tan to light brown with green undertones, tomentulose; peduncle tomentulose; megasporophylls with depressed central narrowly elliptic facet and margins folded back axially, 2.4 cm wide, 1.0 cm high. Seeds 2.8-3.0 cm long, 1.6-1.8 cm wide, bright red, not visible between undehisced megasporophylls when mature. Chromosome number $2n=20$.

Etymology. The species is named for its extremely elegant appearance, large cultivated specimens bearing up to 40 or more large, shining, rather upright leaves. The beauty of these plants has made them prized elements in cycad collections.

Distribution and Ecology. Plants have been observed in primary lowland rainforest as well as secondary and other disturbed habitats. Strobili seem to occur more frequently on plants along stream banks where light conditions are better, and negligible in the forest understory, except in treefall areas where light could penetrate the canopy. All plants observed with strobili were female. The low rate of reproduction in *Zamia elegantissima* is in contrast to *Z. fairchildiana* populations, which seem to be actively reproducing even in shaded habitats. In those populations, large numbers of coning specimens of both sexes were observed (R.S. Adams, pers. obs.). Dr. Alberto Taylor (1999) of the Universidad de Panamá reports extremely high seedling mortality in natural habitats.

Populations of *Zamia elegantissima* are extremely variable with respect to plant mature size and strobilus size. Coning female specimens have been observed with as little caudex girth as 5-10 cm. Individual female plant size is uncorrelated with strobilar size. Seed germination is also unusual in that the seeds seem to lack the inhibitors present in the sarcotesta of many cycad species. This allows ripe seed of *Zamia elegantissima* to germinate quickly in the presence of adequate moisture after dehiscence, rather than after various external factors result in the disintegration and/or disappearance of the sarcotesta. Coleorrhizae emerged directly through the sarcotestas within a few days after being placed in water. Coleorrhizae of the latest seeds collected were already breaking through the sarcotesta before even falling to the ground.

Taxonomic relationships. The description of *Zamia elegantissima* increases to six the number of related species in Schutzman's (1998) putative *Z. fairchildiana* species group, which also includes *Z. acuminata* Oersted *ex* Dyer, *Z. fairchildiana* L.D. Gómez, *Z. inermis* Vovides & Rees, *Z. obliqua* A. Braun, *Z. soconuscensis*

Schutzman, Vovides, & Dehgan, and *Z. tuerckheimii* J. Donn. Sm. The South American species *Z. encephalartoides* D.W. Stevenson and two undescribed species from Honduras and Belize appear to belong to this group, and would increase the count to nine. We consider *Z. pseudomonticola* to be conspecific with *Z. fairchildiana* as it differs in only one leaflet feature, which we believe to vary in a continuum between the extremes seen in several populations. It is conceivable that Gómez had not seen more than three populations *in toto*, as his publication only lists one specimen for *Z. pseudomonticola*, and two for *Z. fairchildiana*. Herbarium specimens annotated later by Gómez as *Z. pseudomonticola* are within our species concept of *Z. fairchildiana*.

Gómez has annotated other specimens of both Costa Rican and Panamanian origin as *Zamia fairchildiana*. The Panamanian populations near the Costa Rican border belong to *Z. fairchildiana*, but are disjunct and morphologically distinct from the central Panamanian plants, belonging in *Z. elegantissima*. The two species are alike in that plants of both may be large, pachycaulous and arborescent, and possess large strobili.

Leaf number and habit. Leaves of *Zamia elegantissima* are numerous both in habitat and in cultivation, often more than 30 in cultivation and erect, while those of *Z. fairchildiana* number 20 or fewer, and are arching. In habitat, we would expect leaf number to be correlated with light, soil and moisture conditions as they affect plant vigor. Leaves of the Guatemalan and Honduran species *Z. tuerckheimii* leaves are numerous and widely arching.

Reproductive features. Microsporophyll faces of *Zamia elegantissima* as well as *Z. tuerckheimii* are pointed as compared to the more blunt hexagonal faces of *Z. fairchildiana* microsporophylls; the faces of *Z. elegantissima* microsporophylls are still hexagonal, only much smaller and seemingly protuberant (Figures 4a-d).

Megastrobili of *Zamia fairchildiana* possess from 5 to 12 vertical rows of megasporophylls, whereas those of *Z. elegantissima* were much longer, possessing from 14 to 20 rows. A significant difference between the two species is the visibility of ripe seed in undehisced megastrobili; in *Z. fairchildiana*, seed are visible and their enlargement pushes the megasporophylls far apart (Figure 5), similar to the situation in *Z. tuerckheimii*, while the ripe seed of *Z. elegantissima* do not become visible until the disintegration of the megastrobilus. Megasporophylls are easily distinguished, those of *Z. fairchildiana* similar to *Z. tuerckheimii* and many other zamias in their relative flatness with some undulation at the peltate margin and a rather hexagonal face, while the *Z. elegantissima* megasporophyll has a margin folded back toward the strobilar axis, and a deep linear indentation in the face (Figure 1j,k). Color of *Z. fairchildiana* megastrobili vary from light cream to tan to light brown due to variation in color of trichomes along with a varying amount of green underlying color from the megasporophylls themselves. Those of *Z. tuerckheimii* are tan to dark brown, but also have a green underlying megasporophyll color. The megastrobili of *Z. elegantissima* are lighter in color, ranging from cream through yellowish to tan.

Zamia fairchildiana is one of three species known to possess microsporangia on both ad- and abaxial microsporophyll surfaces. Another is *Z. cunaria* Stevenson & Dressler, a subterranean species from central Panamá, and the third is a yet undescribed species reported by D.W. Stevenson (1999) from Colombia.

Microsporophylls of *Z. elegantissima* only bear microsporangia on the abaxial surface, as do most other known *Zamia* species (Figure 3A). Additionally, *Z. fairchildiana* microsporophylls bear microsporangia over the entire abaxial surface of the microsporophyll, lacking the interstitial area which splits the fertile region into two areas (Figure 4C left), whereas in *Z. elegantissima*, this interstitial area may be greatly reduced but still is present at least near the microsporophyll apex. The interstitial area of *Z. tuerckheimii* microsporophylls is much wider, similar to that of most other *Zamia* species.

Stem. Trunk size differs substantially between and among populations of both *Zamia fairchildiana* and *Z. elegantissima*, most likely depending heavily upon environmental conditions. Stems of *Z. elegantissima*, though extending above ground, always are found to possess at least 15 cm of their stem length below the ground, when soil is ample enough to make this physically possible (A. Taylor, pers. comm.). Girth of stems is also a variable feature and overlaps significantly between the species. Stems of *Z. tuerckheimii* are often decumbent with as much or more trunk on the ground as extends upward.

Leaf characters. Petioles of *Zamia fairchildiana* appear to be covered with dark brown tomentum when emerging, and these appear lighter when the leaf is fully expanded. Petioles of *Z. tuerckheimii* and *Z. elegantissima* are both glabrous when emerging and are bright green. Those of both *Z. elegantissima* and *Z. fairchildiana* seedlings are prickly, but petioles of older specimens of *Z. elegantissima* gradually become smoother until very few prickles are seen.

Leaflet characteristics (Figure 4). Leaflets of *Zamia elegantissima* are somewhat falcate with marginal teeth beginning at the apex and usually extending somewhat below the midpoint, though in some cases, tothing may be almost absent. This feature often changes from one flush of growth to another. These leaflets also lack the conspicuous longitudinal creasing present in *Z. fairchildiana* leaflets. The leaflets of *Z. fairchildiana* are sigmoidal (curving in two directions), toothed sparingly only at the apex, and with conspicuous longitudinal convex crease. This creasing was first reported by Schutzman in *Z. standleyi* (1990), and also occurs in several other species including *Z. lindenii* and *Z. acuminata*, but tends to be lost in all of these species when herbarium specimens are made. The leaflets of *Z. fairchildiana* vary significantly from population to population. Those closer to Panamá tend to possess a long-acuminate apex, often referred to as a "drip-tip." It is these plants with the abrupt but long acuminate apices that have been sporadically identified as *Z. pseudomonticola*. The plants at the type locality of *Z. fairchildiana* do not have an abrupt but elongate acuminate apex like those in more localities further east. *Zamia tuerckheimii* leaflets have a shape similar to and as variable as those of *Z. fairchildiana*, but do not possess the longitudinal convex crease. The color of *Z. elegantissima* leaflets is darker than that of *Z. fairchildiana* and similar to that of *Z. tuerckheimii*, but new growth of all three species is similarly a very light shade of green. No populations of any of the taxa tentatively thought to belong to this species group are known to possess plants with bronze or pink-emerging leaves, a feature common in other Mesoamerican and Caribbean taxa such as *Z. spartea* A.DC., *Z. loddigesii* Miq., *Z. splendens* Schutzman, *Z. standleyi* Schutzman, *Z. crennophila*, *Z. lacandona*, *Z. purpurea* Vovides, Rees, & Vazquez-Torres, and the *Zamia* species from the Bahamian islands of New Providence, Long Island, and Eleuthera.

Chromosome number. *Zamia elegantissima* has $2n=20$, the first report of that diploid number in *Zamia*. Chromosome numbers for other members of the tentative species group are not well-known. Norstog (1980) reports $2n=18$ for *Z. obliqua*. Diploid number for *Z. tuerckheimii* is not known because the diploid number given for *Z. tuerckheimii* in Norstog's (1980) paper is actually that of *Z. standleyi* (voucher K. Norstog #80-3 from accession #FTG76-977). Both *Z. soconuscensis* and *Z. inermis* have $2n=16$. This diversity in diploid chromosome number is quite unlike that seen in the *Z. splendens* group, in which all known species have $2n=16$, though *Z. lacandona* also was found to have $2n=17$ and 18 (Schutzman *et al.* 1998).

Seedling morphology. *Zamia elegantissima* seedlings are easily distinguishable from those of *Z. fairchildiana*. Eophylls (first leaves) of *Z. elegantissima* possess three or four leaflets and are 3-6" tall, while those of *Z. fairchildiana* hold two or rarely three leaflets and can be 8-12" tall. *Zamia tuerckheimii* seedlings have not been observed.

Other specimens observed. PANAMA. Canal Zone: *Muenschner 12089* (BH); *Muenschner 16240* (BH); *Gentry 8683* (MO); *Woodson, Allen, & Seibert 1596* (GH,MO). Colon: *Croai 14176* (MO). Panamá: *Nee 9299* (MO).

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LITERATURE CITED

- Gómez, L.D. 1982. *Plantae mesoamericanae novae*. II. *Phytologia* 50:401-404.
- King, M. 1993. *Species Evolution: The Role of Chromosome Change*. Cambridge University Press, New York, New York.
- Levan, A., K. Fredga, & A.A. Sandberg. 1964. Nomenclature for centromeric position on chromosomes. *Hereditas* 52:201-220.
- Lima-de-Faria, A. 1983. *Molecular Evolution and Organization of the Chromosome*. Elsevier, Amsterdam, New York, Oxford.
- Moretti, A. 1990. Karyotypic data on north and central American Zamiaceae (Cycadales) and their phylogenetic implications. *Amer. J. Bot.* 77:1016-1029.
- Moretti, A. & S. Sabato. 1984. Karyotype evolution by centromeric fission in *Zamia* (Cycadales). *Plant Syst. Evol.* 146:215-223.
- Norstog, K. 1980. Chromosome numbers in *Zamia* (Cycadales). *Caryologia* 33:419-428.
- Schutzman, B. 1984. A new species of *Zamia* L. (Zamiaceae, Cycadales) from Chiapas, Mexico. *Phytologia* 55:299-304.
- _____. 1989. A new species of *Zamia* from Honduras. *Syst. Bot* 14:214-219.

- ____ & A.P. Vovides. 1998. A new *Zamia* (Zamiaceae, Cycadales) from Eastern Chiapas, Mexico. *Novon* 8:441-446.
- ____, A.P. Vovides, & B. Dehgan. 1988. Two new species of *Zamia* (Zamiaceae, Cycadales) from Southern Mexico. *Bot. Gaz. (Crawfordsville)* 149:347-360.
- Stevenson, D.W. 1993. The Zamiaceae in Panama with comments on phytogeography and species relationships. *Brittonia* 45:1-16.
- Taylor, A.S. 1999. Insect herbivore relationship in natural reproductive *Zamia* populations in Panama. Paper presented at the Fifth International Conference on Cycad Biology, Miami, Florida, August 7-10.
- Vovides, A.P. 1983. Systematic studies on the Mexican Zamiaceae. I. Chromosome numbers and karyotypes. *Amer. J. Bot.* 70:1002-1006.
- ____ & M. Olivares. 1996. Karyotype polymorphism in the cycad *Zamia-loddigesii* (Zamiaceae) of the Yucatan Peninsula, Mexico. *Bot. J. Linn. Soc.* 120:77-83